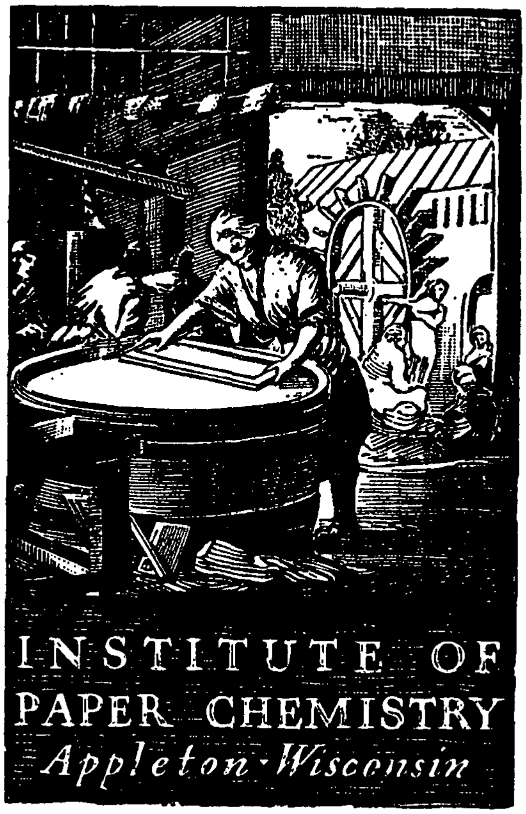

A STUDY OF THE GENETIC IMPROVEMENT OF QUAKING AND BIGTOOTH ASPEN BY SELECTION, HYBRIDIZATION, AND THE EXPLOITATION OF POLYPLOIDY

Project 2412

Report Two

A Progress Report

to

LOUIS W. AND MAUD HILL FAMILY FOUNDATION

May 20, 1965

THE INSTITUTE OF PAPER CHEMISTRY

Appleton, Wisconsin

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SUMMARY

1. The selection of outstanding trees from natural stands and progeny ɔ:; continued. Promising among the several trees selected were a male and fe- cottonwood with good form and rate of growth from Central Wisconsin.

2. A rapid-growing triploid aspen clone was discovered during the past through the co-operation of the Minnesota and Ontario Paper Company. Located International Falls, Minnesota, the clone had produced approximately 110 cords acre in 43 years.

3. An experimental cross made in 1958 employed a tetraploid tree from en as a male parent and an outstanding diploid from Upper Michigan as a fe- parent. The progeny produced were triploids and have shown good growth and wood quality. This cross was repeated and 3,300 triploid seedlings were pro- d in order that the cross be more widely tested.

4. A new colchicine treatment technique was developed for use in the uction of quaking aspen tetraploids. This technique involves treating newly ıed embryos when they are made up of relatively few cells. A number of very nising "tentative tetraploids" were produced.

5. Thirty-six experimental crosses were made during the 1964 crossing son. Twenty-eight parent trees were employed and major emphasis was placed on production of bigtooth aspen crosses and bigtooth aspen hybrids suitable for y sites."

6. The field work phases of the previously described study on "Geographic Variation of Quaking Aspen" were completed and the data on tree growth, soils, and wood properties are in the process of being tabulated. The specific gravity data indicates a north-south trend of decreasing specific gravity with increasing latitude.

7. Results obtained in two additional studies of natural variation are described. Included is information obtained on the reasons for specific gravity variability encountered in 5-year-old aspen seedlings.

INTRODUCTION

The basic objectives of Project 2412 are to discover ways of increasing the per acre production of usable wood and to improve the quality of the wood produced. The principal techniques that are being employed are selection, hybridization, and polyploidy. Selection involves locating parent trees which have the characteristics desired and propagating these individuals vegetatively. Hybridization consists of mating two trees of unlike genetic make-up and has the advantage that it is possible to produce genetic combinations that would not normally occur in nature. Polyploidy involves the production of individuals which have extra sets of hereditary units in each cell nucleus.

Heritability, natural variation, and importance to the end product being produced are factors that must be considered when determining those wood, morphological, and biochemical characteristics of a tree that are worthy of genetic improvement. Heritability is a measure of the relative degree to which a characteristic is influenced by its heredity as contrasted to its environment. To illustrate the importance of heritability information, let us say that by careful selection we can obtain two parent trees that have fiber lengths that are 20% longer than average. If the heritability of fiber length is 60%, this means that 60% of the gain obtained by selection will be passed on to the progeny produced by crossing the two selected trees. The expected gain in this case would be a 12% increase in fiber length.

Natural variation is also important, as was shown in the previous illustration, because variation also influences the genetic gains that can be obtained. If natural variation had been quite low, and by careful selection we had obtained parent trees that had only 5% longer fibers, the expected genetic gain would have been only 3% despite a relatively high heritability.

The importance of the characteristics being improved to the end product being produced must also be considered. If moderate increases in fiber length greatly improve sheet properties, this may make the sheet useful in a higher value product or require less fiber to meet the strength requirements and may make genetic gains quite desirable. If, however, the characteristic involved does not increase the value of the end product or reduce the production costs, attempts to genetically improve such a characteristic might best be forgotten.

The report that follows covers the period from January 1, 1964 to December 31, 1964 and describes the work under way with several species of Populus in the areas of selection, hybridization, and polyploidy. Also included are descriptions of studies that have been established to increase our knowledge of natural variation, and heritability.

SECURING AND PROPAGATING DESIRABLE POLYPLOID AND DIPLOID ASPEN

SELECTION - OUTSTANDING TREES LOCATED DURING THE PAST YEAR

Selection of parent trees on the basis of wood, growth, and morphological characteristics is a necessary first step in any tree improvement program. Each year 30 to 40 individuals are measured and evaluated. Those trees that meet the minimum standards for all characteristics and are outstanding in at least one or two characteristics are selected for use as parent trees in future hybridization and polyploid studies. A selection index system employing a numerical rating method is used. The trees that survive this initial selection are next checked for their flowering and crossing behavior and then finally evaluated on the basis of the quality and vigor of the progeny produced. Listed and described below are five of the better trees evaluated during the past year. These trees are now in the process of being compared on the basis of their crossing behavior.

Tree D-1-63

Tree D-1-63 is an eastern cottonwood, *Populus deltoides*, located several miles west of Waupaca, Wisconsin. This tree is a male and is growing in a sandy depression just south of Wisconsin State Highway 54. D-1-63 is open grown and is not exceptional in size but was selected because of its narrow crown and straight unbranched main stem. The growth, form, and wood quality information available on the above tree is as follows:

Total height - 62 feet	Diameter breast height - 9.9 inches
Height to 3 inch top - 35 feet	Diameter 16.5 feet - 7.4 inches
Height first live branch - 26 feet	B.h. bark thickness - .73 inch
Age - 19	Crown diameter - 13 feet
Stem straightness - good	No. major branches - 19
Natural pruning - very poor	Branch angle - 70°
Branch weight - good	Form factor - 61
Specific gravity - .372 g./cc.	
Fiber length (age 15) - .892 mm.	

Tree D-6-65

Tree D-6-65, pictured in Fig. 1, is a male eastern cottonwood (*Populus deltoides*) located in northern Outagamie County approximately two miles east of the town of Nichols, Wisconsin. The soil is sandy and poorly drained and the tree involved is one of several rapidly growing cottonwoods located on this moist site. The tree was selected for its outstanding size and very good form. The information on growth and form of D-6-65 is as follows:

Total height – 77 feet

Height to 3 inch top – 58 feet

Height first live branch – 39 feet

Age – 42 years

Stem straightness – good

Natural pruning – good

Branch weight – good

Specific gravity – .358 g./cc.

Fiber length (age 30) – .93 mm.

Diameter breast height – 19.7 inches

Diameter 16.5 feet – 15.8 inches

B.h. bark thickness – .75 inch

Crown diameter – 25 feet

No. major branches – 17

Branch angle – 70°

Form factor – 75

Tree G-1-65

Tree G-1-65 is a male bigtooth aspen, *Populus grandidentata*, that is a member of a clone of trees growing on shallow sandy soils near Anderson Lake in Oconto County. This tree and the other trees of this clone have good form and appear to be growing much better than the other aspen located in nearby stands. This tree was selected primarily because of its apparent ability to grow well on dry, infertile sandy soils. Additional study of the site is planned to verify subsurface soil conditions. The wood, growth, and morphological characteristics available for G-1-65 are as follows:

Figure 1. The Cottonwood Being Sampled (D-6-65) is 42 Years Old and Has the Straightness and Natural Pruning Desired in Cottonwood Parent Trees. The Tree in the Center of the Picture Illustrates the Heavy Branching and Wide Crown Typical of Most Cottonwood in Wisconsin

Total height – 80 feet

Height to 3 inch top – 60 feet

Height first live branch – 50 feet

Age – 52 years

Stem straightness – good

Natural pruning – good

Branch weight – good

Specific gravity – .368 g./cc.

Fiber length (age 30) – .853 mm.

Diameter breast height – 11.4 inches

Diameter 16.5 feet – 10.0 inches

B.h. bark thickness – .40 inch

Crown diameter – 13.0 feet

No. major branches – 6

Branch angle – 55-60°

Form factor – 82.1

Tree XT-12-58, S-1

Tree XT-12-58, S-1, shown in Fig. 2, is a young quaking aspen (Populus tremuloides) that was produced by crossing two good quaking aspen parent trees. The tree was planted out in 1959 as a one-year-old seedling (Experimental Trial X) on the Ripco Experimental Area located in Oneida County, Wisconsin. Part of the trees in Experimental Trial X were sampled to obtain wood quality information when the planting was five years old. Prior to cutting, XT-12-58, S-1, was measured and selected for further study on the basis of its satisfactory growth, good form, and good natural pruning. Wood quality information obtained after cutting indicates the tree has good specific gravity, strong fiber strength and a little below normal fiber length. The wood, fiber, and growth characteristics of this selected tree are as follows:

Total height – 18 feet

Height to 3 inch top – Not available

Height first live branch – Not available

Age – 5 years

Diameter breast height – 2.0 inches

Diameter 16.5 feet – Not available

B.h. bark thickness – Not available

Crown diameter – 8.0 feet

Figure 2. This Five-Year Old Quaking Aspen (XT-12-58, S-1) Is 18 Feet Tall, Has Good Straightness and Natural Pruning. Pulp Evaluation Studies Revealed The Tree Has Very High Fiber Strength

em straightness - good

tural pruning - very good

anch weight - good

pecific gravity - .370 g./cc.

iber length (age 5) - .509 mm.

iber length (age 30) - .820 mm.

iber strength - 73.6 lb./in.

No. major branches - 19

Branch angle - 80°

Form factor - Not available

Tree XT-22-56, S-2

The above selected tree is a young quaking aspen (*Populus tremuloides*) that was produced by crossing two outstanding parent trees from Upper Michigan. The average growth of this experimental cross has been good on all areas where it has been planted and XT-22-56, S-2, is one of the better individuals from this cross. This selected tree was field planted in 1958 as part of Experimental Trial VII (Greenville Test Area) and was cut as part of a wood quality study after it had grown for 5 years in the trial. The tree demonstrated exceptional height and diameter growth, had good form and satisfactory wood quality. The data on growth, form, and wood quality for XT-22-56, S-2, are as follows:

Total height – 20.5 feet

Height to 3 inch top – Not available

Height first live branch – Not available

Age – 5 years

Stem straightness – very good

Natural pruning – very good

Branch weight – average

Specific gravity – .373 g./cc.

Fiber length (age 5) – .72 mm.

Fiber length (age 30) – 1.045 mm.

Fiber strength – 61.2 lb./in.

Diameter breast height – 2.0 inches

Diameter 16.5 feet – Not available

B.h. bark thickness – Not available

Crown diameter – 9.0 feet

No. major branches – 17

Branch angle – 60°

Form factor – Not available

DISCOVERY AND PRODUCTION OF TRIPLOID ASPEN

Triploid quaking aspen are individuals that have three sets instead of the normal two sets of hereditary units in each cell nucleus.* Such trees are of interest because it has been demonstrated that triploids have longer fibers and grow faster than normal diploid trees [van Buijtenen, et al., (1)]. Each year a limited amount of time is spent examining aspen of unusual size and rate of growth in an effort to locate additional triploid clones.** During 1964 one new triploid clone was sampled and verified. This quaking aspen clone was discovered by Mr. Arthur Ennis of Minnesota and Ontario Paper Company and is located approximately 15 miles southwest of International Falls, Minnesota. Measurements on this clone have not been completed and only one tree, T-1-65, has been checked for chromosome numbers. Based upon the limited measurements and wood samples supplied by Mr. Ennis, this clone appears to be the fastest growing group of aspen we have identified as triploid.

Measurements made in 1960 when the clone was 43 years old, indicated the area had a total of 110 cords per area. This is two to three times the volume of fast-growing aspen stands of similar age in northern Wisconsin. The larger trees in this clone range from 13 to 20 inches in diameter and from 97 to 102 feet tall. Included in Table I is a brief summary of the growth and wood quality information that was obtained from T-1-65, one of the trees from this clone. The fiber length

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* The normal diploid or 2*n* chromosome number is 38, the triploid or 3*n* number is 57 and the tetraploid or 4*n* number is 76.

** A clone is a group of individuals derived from a single individual by asexual reproduction. In natural stands of aspen, the clones have been produced from the root system of a single individual by root suckering - usually after fire, cutting, or similar injury.

information indicates that the tree has the typical long fiber (20 to 30% longe than normal) associated with triploid aspen. The other wood and pulp propertie are about average or a little above.

TABLE I

SUMMARY OF GROWTH AND WOOD PROPERTIES OF TRIPLOID T-1-65

Height - 97.5 feet	Fiber strength - 65.9 lb./in.
Height, 4 in. top - 82 feet	Age (1964) - 47 years
Diameter at 4.5 feet - 13.3 inches	Pulp yield - 51.8%
Specific gravity - 0.372 g./cc.	Lignin - 17.4%
Fiber length (age 30) - 1.24 mm.	Extractives - 3.6%

During the last three years, considerable emphasis has been placed on (1) vegetative propagation and testing of existing natural and artificially produced triploids, and (2) mass production of triploid aspen seedling. As a resul of this switch in emphasis, the production of triploid aspen seedlings and root sprouts increased during the past year. Vegetative propagation of the ten tripl aspen clones listed in Table II was started in 1963 and the trees were lined out and grown in the nursery during 1963 and 1964. These trees have reached a size suitable for field planting and seven of the ten triploid clones and one diploi aspen clone will be planted in a replicated trial at the Ripco Experimental Farm in the spring of 1965.

A second method of producing triploid material, in addition to vegetative propagation, consists of crossing a tree that has four sets of hereditary units (4<u>n</u>) with a tree that has a normal two sets of hereditary units (2<u>n</u>). A high percentage of the resulting progeny from a cross of this nature are triploid

(3*n*) individuals. The use of the "tetraploid x diploid" crossing technique was tried at the Institute in 1958 and several crosses containing a high percentage of triploid individuals were produced. Progeny from one of these crosses (XT-Ta-14-58) has produced satisfactory growth and the wood and fiber properties are also well above average. Figure 3 illustrates the size attained by the triploid progeny of this cross. Three of the best individuals from this cross have been selected for vegetative propagation and, during the past year, cross XT-Ta-14-58 was repeated* and approximately 3,300 plantable triploid seedlings were produced. These seedlings had as a female parent an outstanding diploid (2*n*) tree T-1-58 from the Porcupine Mountains in Upper Michigan and as a male parent, a tetraploid (4*n*) tree of Swedish origin.** Extensive testing is planned with this group of seedlings and it is hoped that additional outstanding individuals can be selected that will be of value in future vegetative propagation work.

PRODUCTION OF TETRAPLOID ASPEN

Evidence, based upon work done in Europe with European aspen and closely related species, indicates that tetraploid individuals are slow growing and not in themselves desirable individuals. Tetraploids are useful, as the preceding topic on "production of triploids" indicates, as parents in controlled crosses made for the purpose of mass producing triploid seedlings. One disadvantage in the use of pollen from the Swedish tetraploid is that this tree grows at a latitude approximately equivalent to that of Churchill, Manitoba on Hudson Bay in Canada. Bringing

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*The new cross number is XT-Ta-6-64 and details of this cross can be obtained from Tables IX and X of this report.

**Pollen obtained through the courtesy of Dr. Helge Johnsson, Swedish Forest Tree Breeding Institute, Ekebo, Sweden.

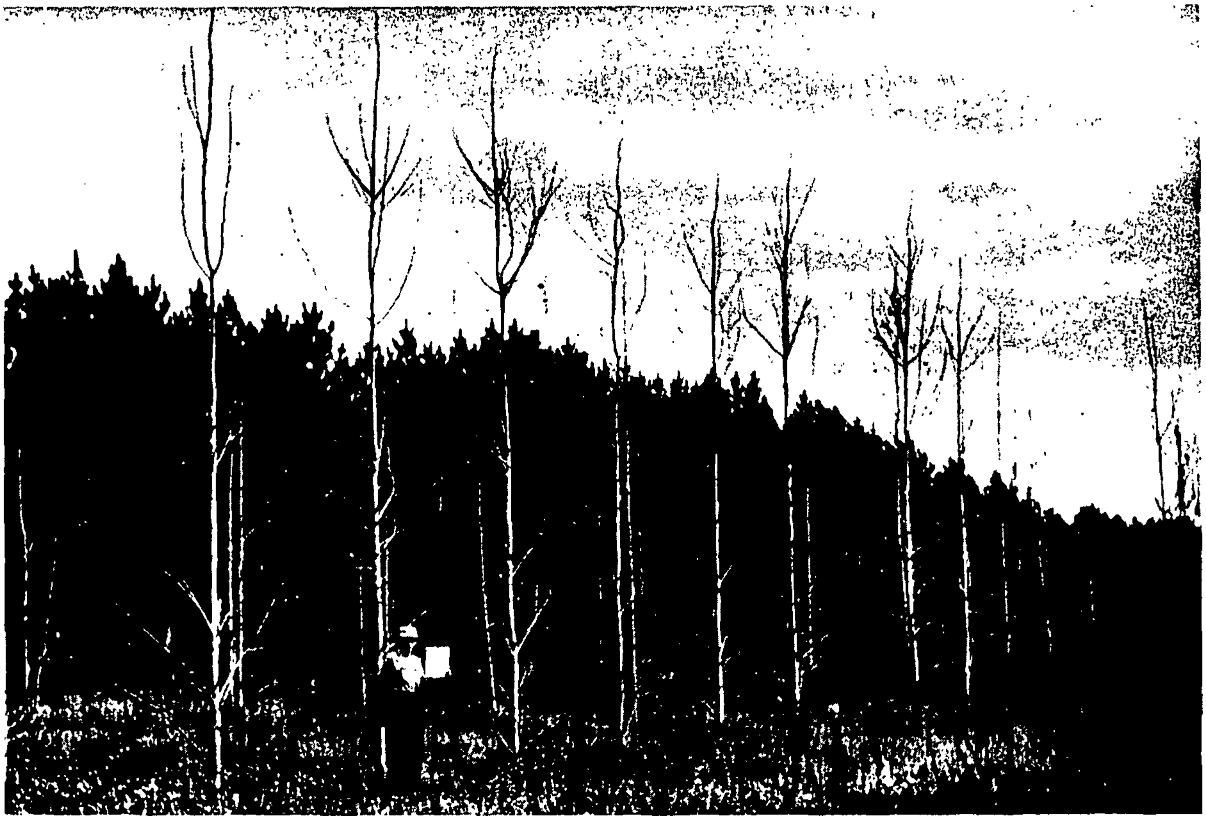

Figure 3. Dr. Ralph Anderson, Lake States Forest Expt. Station Examining Progeny of XT-Ta-14-58, a Triploid Hybrid Growing at the Ripco Expt. Farm. After Six Growing Seasons the Seedlings Shown Above Average Approximately 26 Feet Tall and 3 Inches in Diameter. This Cross Has Been Repeated and Wider Testing is Anticipated

a tree south often results in the tree having, as part of its genetic make-up, a time of spring flushing and fall dormancy suited for the northern climate and this results in the tree utilizing only a part of the available growing season at the new southern location. The point of this discussion is that it would be very desirable to have available a tetraploid of local origin, well adapted to the present Lake States climate for use in the production of triploids.

TABLE II

PROPAGATION OF TRIPLOID CLONES

Clone Number	Location of Clone	Number Individuals Propagated
T-2-56	Bruce Crossing, Mich. Area No. 1	53
T-36-56	Bruce Crossing, Mich. Area No. 1	149
T-71-57	Bruce Crossing, Mich. Area No. 2	191
T-7-59	Bruce Crossing, Mich. Area No. 3	216
T-9-59	Bruce Crossing, Mich. Area No. 3	115
T-38-59	Trout Creek, Mich.	178
T-43-59	Barrie Island, Lake Huron (Canada)	188
T-1-62	Chippewa Falls, Wis.	152
XT-Ta-14-58 S-1	Expt. Triploid Hybrid Ripco Farm	113
XT-Ta-14-58 S-2	Expt. Triploid Hybrid Ripco Farm	98
XT-12-58 S-1	Expt. Diploid Tree Ripco Farm Used as Control	113

A literature review in this area of research indicated several techniques were available for the production of tetraploids and the following seemed to be the most appropriate for use with forest trees.

1. Colchicine treatment of germinating seed.
2. Colchicine treatment of newly formed embryos.
3. Hybridization using polyploid parents.

<u>Colchicine Treatment of Germinating Seed</u>

Colchicine treatment of germinating seed has been under investigation at the Institute for several years and a number of aspen and cottonwood triploid prospects have been obtained. The principal disadvantage of the use of this technique is that often only a portion of the seedling has a double chromosome number. The normal diploid tissue usually outgrows the tetraploid tissue. In cases where a seedling is part diploid and part tetraploid, the seedling, upon growth, will have a higher and higher proportion of diploid tissue. This necessitates constant checking and rechecking of the tetraploid prospects until they begin to flower. No work was done in this area this past year other than the rechecking of a number of earlier treated individuals. For additional details on the work completed using this technique, the reader is referred to Project 2412, Progress Report 1.

<u>Colchicine Treatment of Newly Formed Embryos</u>

Colchicine treatment of newly formed embryos has not been widely used with forest trees. Such a technique has the obvious advantage that, if the timing of the treatment is right, fewer cells would be involved and the chances of obtaining completely tetraploid individuals are increased. The information that follows describes the techniques used and the results obtained when this method was tried on quaking aspen.

The procedure employed was to make two experimental crosses (XT-1-64 and XT-5-64) using the standard "cut branch" technique. The female catkins were pollinated and the pollinated catkins were immersed in a solution of 0.3% colchicine. The treatment was applied for a total of six hours and was started at periods of 6, 12, 18, 24, and 30 hours after pollination.

The treated catkins were carried through to maturity and the seed produced was separated by size and germinated using the "IPC seed saucer technique." The seedlings produced were examined periodically and transplanted when approximately 1/2 to 3/4 of an inch in height. Chromosome counts were made on the transplanted seedlings when they were 3 to 5 inches in height. In experimental cross XT-1-64, large numbers of seed were obtained in the 24 and 30-hour treatments and only abnormal appearing seedlings were transplanted and checked for chromosome number. Descriptions were made of a number of abnormal individuals with the hope that the information gained on treatment times, seed size, and nature of abnormalities would be useful in future studies with quaking aspen and other species within the genus *Populus*.

Table III provides a summary of the treatments used as well as the numbers of putative polyploids recovered. Megaspore* development was more seriously inhibited by the colchicine treatments in experimental cross XT-5-64. The reason for the greater injury is not known. The same female parent was used in both crosses and, although the crosses were made four weeks apart, environmental conditions were equally favorable. Variation in the stage of megaspore development at the time of treatment suggests one possible explanation. Female catkins of *P. tremuloides* usually remain receptive for 36 to 48 hours, and it is possible that the catkins in cross XT-5-64 were less advanced and the megaspores more easily injured at the time of treatment. Another possibility is that pollen from the male parent involved in cross XT-5-64 was less compatible and/or pollen tube development was slower than in cross XT-1-64.

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*Female cells produced by meiosis (reduction division) during sexual reproduction of seed plant.

Preliminary chromosome counts obtained from seedlings produced by the treatment described above are very encouraging. Many plants were obtained in which most cells examined had chromosome numbers approximately equal to the tetraploid number of 76. Uniformly high chromosome counts are important because this indicates that most, if not all, of the cells of the newly formed embryo have been influenced by the colchicine treatment.

The results of this initial study show that treating aspen catkins with colchicine six hours after pollination produced satisfactory numbers of putative tetraploids. More work will be required to find the optimum elapsed time after pollination to initiate the colchicine treatment, and the best duration of treatment. Putative tetraploids will be rechecked during the 1965 (second) growing season. It is hoped that new cytotechniques, now being developed, may help confirm the exact levels of ploidy.

One unexpected development was the production of a number of individuals which appeared to have a high proportion of triploid cells. The manner in which triploids arise from the treatment described is not entirely clear, and can only be explained by careful cytological investigations. Premature application of colchicine and the doubling of the chromosome number of either the male generative nuclei or the female gametes, or both, could account for chromosome numbers obtained. Cytological studies into the mechanism of aspen fertilization are now under way. Another interesting aspect of this study was that the growth of the putative tetraploids produced by treating young embryos was much better than that of mixaploids produced earlier by treating germinating seeds and young seedlings. The genetic balance resulting from all cells of a plant being tetraploid could account for the better growth observed.

TABLE III

SUMMARY OF COLCHICINE TREATMENT AND CHROMOSOME COUNT DATA

Treatment[a]	No. Catkins Treated	Seed Size (mesh)	Total No. Seedlings Produced	Total No. Seedlings Counted	Putative Tetraploids[b] Number	Putative Tetraploids[b] %
			XT-1-64			
6	2	28	1	1	0	0
		40	29	27	12	44
12	3	40	3	2	1	50
18	3	28	2	1	0	0
		40	37	31	9	29
		60	1	1	1	100
24	3	28	22	20	3	15
		40	422[c]	16	7	44[c]
30	2	28	14	14	2	14
		40	206[c]	8	4	50[c]
			XT-5-64			
6	3	40	14	12	7	58
12	3	40	4	4	0	0
		50	13	11	3	27
18	3	40	3	3	1	33
24	3	40	0	–	0	0
30	3	40 & 50	5	3	0	0

[a]Six-hour treatment of 0.3% colchicine applied at 6, 12, 18, 24, and 30 hours after pollination.

[b]Putative tetraploids — based upon 8-12 cell counts per seedling. One or two cells were allowed with counts of 60-65. The remaining cells had an average chromosome number of 76 (tetraploid).

[c]Normal appearing seedlings were discarded and the counts were restricted to aberrant seedlings.

The seed-size information available indicates that large seeds (28 mesh) did not produce as high a per cent of putative tetraploids as the smaller seeds (40, 50, 60 mesh). The 40-mesh seed, which is the most common size obtained when the catkins are not chemically treated, produced the highest proportion of putative tetraploids. It also appears that the selection of abnormal seedlings can be used as a preliminary screening technique to decrease the total number of individuals subsequently examined for chromosome number.

Hybridization Using Polyploid Parents

The third technique, in which there is some possibility of producing tetraploid individuals, involves hybridizing polyploid trees. Male and female gametes (sperm and egg cells) normally have a single set of chromosomes (1*n*). The production gametes having 2*n* chromosome numbers are rare under normal diploid conditions. Even rarer is the possibility of the fertilization of a 2*n* female gamete with a 2*n* male gamete. The chances of obtaining a tetraploid individual are greatly increased when polyploid individuals are hybridized.

Available to the aspen program was a triploid quaking aspen female growing in Upper Michigan and a tetraploid European aspen male growing in Sweden. The triploid female was expected to provide egg cells (female gametes), the majority of which would range in chromosome number from 1*n* (19) to 2*n* (38). The majority of the female gametes would have chromosome numbers intermediate between 19 and 38, but occasionally one would exist that had a 2*n* number of 38. The tetraploid male would produce male gametes with chromosome numbers from 1*n*+ to 2*n*+. Experience with this particular tetraploid male and evidence from the literature indicates that the majority of the pollen grains that survive are 2*n* (38) in chromosome number. If the above interpretations are correct, this would mean the majority of zygotes produced would be between 3n and 4n.* Because of the imbalance that exists, the zygotes that develop and eventually produce seedlings very likely will have chromosome numbers near 3n and 4n, with those that vary greatly from 3n and 4n being so abnormal that they fail to survive. There is also evidence [Sinnott, Dunn, and Dobzhansky (2)] that the presence of extra chromosomes has less influence and will cause less imbalance at the 4n level than at the 2n level. This then suggests that the hybrids produced from such a cross should contain an occasional 3n individual and the majority of seedlings will have chromosome numbers between 3n and 4n+.

Experimental cross XT-Ta-33-64 was a cross between T-29-57, a triploid female, and Ta-10, a Swedish tetraploid male. As shown in Table IV a total of 209 seeds were produced and although seed germination was below average, a total of 119 seedlings were available for a study of chromosome numbers. The method used in making the chromosome counts [van Buijtenen (3)] involves making squash slides of rapidly growing leaf tissue. The accuracy of this rapid screening method of counting chromosomes is not as high as desired but does make it possible to separate the individuals into several categories based upon chromosome number. In this particular study, the seedlings were placed in the following chromosome number groups: 3n (53-61), 3n+ (62-70), 4n (71-79), and 4n+ (80-plus). Chromosome counts were made on ninety-one trees, and as illustrated in Table IV one tree was classified as 3n, 11 trees were classified as 3n+, 45 trees were classified as 4n and a total of 34 trees were classified as 4n+.

The results obtained were slightly different than expected. The number of individuals that survived was higher than expected and the number of individuals with counts in the 4n+ category was higher than predicted. Many of the seedlings

*The 3n chromosome number for aspen is 57 and the 4n number is 76.

that have chromosome numbers near the 4n number of 76 are growing quite well while many of the 4n+ individuals are stunted and have malformed stems and leaves. Also worthy of mention is the relationship between seed size and chromosome number. Although not conclusive, there was a tendency for there to be fewer individuals with high chromosome members in the seedlings that were produced from the small size seed (50 and 60 mesh).

The major objective of this study was the production of tetraploid individuals for use in future breeding work. With this objective in mind, 30 "putative tetraploids" having uniform chromosome counts were selected for further study. It is planned that these individuals will be grown in large pots and evaluated further using more refined chromosome counting procedures. An additional number (30-60) of the faster growing individuals will be planted at the Greenville Farm and growth observations continued. The over-all results, although somewhat tentative, indicate that the technique is an effective method of producing tetraploid and near tetraploid individuals of the genus Populus.

TABLE IV

SEED AND SEEDLING PRODUCTION AND DEGREE OF POLYPLOIDY IN CROSS XT-TA-33-64[a]

Seed Size	Numbers Produced		No. Seedlings Counted	Number of Seedlings[b]			
	Seeds	Seedlings		3n	3n+	4n	4n+
28	36	17	12	–	–	9	3
40	467	96	73	1	8	33	31
50 & 60	399	6	6	–	3	3	–

[a]Total of 25 catkins pollinated, 24 catkins collected. Total seed production is about 1/5 normal.

[b]The 3n seedlings had between 53 and 61 chromosomes, 3n+ 62 to 70, 4n 71 to 79 and 4n+ 80 or more.

PRODUCTION OF HAPLOID ASPEN

Cells that make up the vegetative portion of a plant normally contain two sets of chromosomes in each cell nucleus. Aspen cells contain two sets of 19 chromosomes or a total of 38. For each chromosome in the set of 19 there is an equivalent or homologous chromosome in the other set. The members of a pair of like chromosomes correspond in size and shape and have groups of genes in the same sequence that control the same sets of characteristics. Theoretically, a tree should be able to grow with just one set of chromosomes. It is of academic and practical interest to determine whether haploid quaking aspen can be produced. After haploid production is achieved, the next step would be to attempt to double the chromosome number back to the normal 38 and in this way produce an individual in which the homologous chromosomes are identical not only in size and shape but are chemically identical. Such a tree (homozygous individual) would be extremely valuable because it would always breed true.

Kimber and Riley, (4) in their review article on "Haploid Angiosperms" cite several methods that have been used in the past to produce haploid individuals. Of the suggested procedures, the use of: (1) weaken pollen technique, and (2) crossing of genetically diverse individuals, seem to be the most appropriate techniques available. The principle involved in both of these techniques is pollination without fertilization. The pollen applied serves only to stimulate the female gamete to develop into a haploid embryo.

The weakened pollen technique was investigated by treating pollen from *Populus alba* with electron irradiation and then using the pollen in an experimental cross with quaking aspen. In such a cross, when the normal diploid hybrid seed results, the seed will be large and the seedlings will have pubescent primary leaves. By discarding the large seeds and counting chromosomes on only the non-pubescent slow-growing individuals from the small-sized seed, the maximum number of good haploid prospects can be checked.

High Voltage Corporation's microwave linear electron accelerator located at their Midwest Irradiation Center at Rockford, Illinois, was used to treat the P. alba pollen. The proposed levels of irradiation were high – 1500 rads, medium – 1000 rads, and low – 500 rads. The accelerator, because of its size, could not be adjusted to give a level irradiation that was low enough to obtain the proposed levels cited above. The accelerator produced approximately 4500 rads on a single pulse. The decision was made to give the pollen samples a 5-second treatment (15 pulses per second) and reduce the irradiation level by placing the pollen samples at varying distances from the center line of the electron beam. The high treatment level was located at a horizontal distance of 2 feet from the center line of the beam, the medium level at a distance of 7 feet, and the low level at a distance of 12 feet. Later calculations indicated that at these distances the irradiation levels of 1325 rads, 100 rads, and less than 10 rads were obtained. The treated pollen was used in experimental crosses XT-A-34-64 (low), XT-A-35-64 (medium), and XT-A-36-64 (high). Untreated control pollen was also available for pollination and examination.

The results of the above crosses, including information on seed production, seed germination, and chromosome counting work are summarized in Table V. The levels of irradiation did not seem to greatly influence the seed production and the seed germination. The most disappointing aspect of this preliminary work was that no germination was obtained on the small-sized seeds. As a result, chromosome counting work was carried out on abnormal individuals located in the 20 and

40-mesh seed classes. Table V indicates the numbers of individuals that were transplanted and counted for chromosome number.

One aspen seedling was produced that had at least a portion of the plant that was haploid. This individual was described as being vinelike when it was small and originally was believed to be entirely haploid. Further checking revealed that a new rapid growing shoot near the base of the seedling was diploid. The origin of this part haploid and part diploid individual is not clear. One possibility is that the seedling originally was haploid and, sometime during development, one of the haploid cells divided abnormally and produced a diploid cell. This diploid cell, because of its normal chromosome number, produced a shoot that outgrew the haploid portion of the plant. Cytological studies are presently under way in hopes of further clarifying the character and origin of the individual obtained. Future plans in this area of investigation include efforts to vegetatively propagate the diploid and haploid portions of the above-described individual and repeat the irradiation trials again in an effort to produce additional haploids.

TABLE V

SUMMARY CROSSES USING IRRADIATED POLLEN

Cross Number	Level of Irradiation	No. Catkins Pollinated	No. Catkins Collected	Seed Size Mesh	No. Seed Produced	Germination, %	Abnormal Seedlings Transpl.	Abnormal Seedlings Counted	Abnormal Seedlings 1n	Abnormal Seedlings 2n
XT-A-34-64	Low (<10 Rads)	3	3	40	300	92	15	10	–	10
				50	3	0				
				60 & 80	500	0				
XT-A-35-64	Medium (100 Rads)	3	3	40	325	92	24	10	1	9
				50	2	0				
				60 & 80	500	0				
XT-A-36-64	High (1325 Rads)	4	4	40	300	92	46	25	–	25
				50	6	0				
				60 & 80	500	0				

STUDIES OF NATURAL VARIATION

HERITABILITY OF WOOD AND GROWTH CHARACTERISTICS OF QUAKING ASPEN

"Heritability," as described earlier in this report, is a measure of the relative degree to which a character is influenced by heredity as compared to environment. Heritability information, when used in conjunction with information on natural variation, makes possible reliable decisions regarding the growth, morphological, and wood properties which can most successfully be modified through tree improvement work.

Experimental Trial VII contains trees from experimental crosses made in 1956, 1957, 1958, and 1959. This trial was established, not only to provide growth and morphological data, but to provide heritability information on wood and fiber properties. The study involves a total of 25 quaking aspen crosses. These crosses were carried out in the Institute's greenhouse and 55 progeny from each cross have been planted in single blocks on a uniform test area at the Greenville Experimental Farm. Figure 4 illustrates one of these blocks of trees from which trees were sampled in 1962.

Plans for this trial include the standard year-by-year growth measurements for the first five years. After the trees have been in the field for five growing seasons, a complete analysis of growth and wood property information will be made. The fifth-year measurements for each experimental cross will include the following: (1) total height - measurements made on all trees, (2) diameter at breast height - measurements made on all trees, (3) straightness of stem - measurements made on all trees, (4) branch angle, length and diameter - measurements made on all trees, (5) number of live branches - measurements made on all trees, (6) natural pruning – measurements made on all trees, (7) specific gravity – 20 trees from each experimental cross to be measured, (8) fiber length information – 10 trees from each experimental cross to be measured, (9) fiber strength (zero-span tensile strength) information – 5 trees from each experimental cross to be measured, and (10) pulping information including pulp yield, per cent extractives, and per cent lignin – 5 trees from each experimental cross to be measured.

Figure 4. Progeny From XT-11-57, Expt. Trial VII. Part of This Cross Was Cut for Wood Quality Evaluation. The Remaining Trees Average 21.0 Feet in Height and 2.0 Inches in Diameter After Seven Growing Seasons

During the past two years, the fifth-year measurements listed above have been completed on 16 of the 25 experimental crosses involved in this study. These data are being tabulated and preliminary analyses are planned. The plans for the study involve completing and tabulating the fifth-year measurements on the remaining nine experimental crosses. On completion of the measurements, the data will be composited and a complete analysis of the study will be made.

The cutting associated with the fifth-year wood property sampling will increase the spacing from the original 3 by 6 foot spacing to a 6 by 6 foot spacing. This spacing will again be increased as growth requires, and additional intensive study of growth, morphological, and wood properties is planned when the trees have been in the field fifteen years.

QUAKING ASPEN GEOGRAPHIC VARIATION STUDY

Project 2412, Progress Report 1, described in some detail the studies established to investigate the geographic variation of quaking aspen. The objectives of this study include increasing our knowledge of the natural variation of wood, fiber, and growth characteristics and accumulating data needed for establishing base lines for judging "wood quality"* of quaking aspen.

The plan adopted was to establish study areas in five geographic locations within the state of Wisconsin and Upper Michigan. Five stands were to be measured in each geographic area and three trees in each of three clones were to

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*Wood quality as referred to in this report refers to the quality of the wood with regard to its use by the pulp and paper industry. Wood properties considered to be important include fiber length, fiber strength, specific gravity, pulp yield, lignin, and extractives.

be sampled in each stand. This sampling resulted in a total of 45 trees being measured in each geographic area. The stands sampled were limited to those growing on medium textured, upland soils with ages of 20 to 45 years. The information to be taken on experimental plots includes: (1) age, form, and rate of growth information on study trees, (2) specific gravity and fiber length based on four 10-millimeter increment cores, (3) soil and other site information based on soil samples taken from the A & B horizons, (4) pulping information based on the micropulping of 4 or 6 10-millimeter increment core samples per tree. Pulping information (fiber strength, pulp yield, extractives, and lignin) was obtained from just one stand within each geographic area.

Extra field time was allotted to this study and the field aspects of the program were completed one year earlier than expected. The data are presently being tabulated and micropulping work is expected to be completed by the first of July. The specific gravity determinations were completed in October and because an interesting trend developed, these data are summarized in Table VI. To illustrate the geographic trend that was obtained, the average specific gravity for each area was recorded on the study area map, Fig. 5.

Table VI illustrates a trend of decreasing specific gravity with increasing latitude. The five stands in the Madison, Wisconsin area had the highest specific gravity (.420) and the three northern areas (Areas C, D, E, shown in Fig. 5) had comparable specific gravity values of .374, .378, and .388. No east-west trend in specific gravity was evident. A statistical analysis of these data indicates that the specific gravity of the stands of area A are significantly higher than the specific gravity of quaking aspen in the other study areas. This information should be taken into consideration when selecting parent trees from southern Wisconsin.

TABLE VI

SUMMARY OF SPECIFIC GRAVITY DATA
GEOGRAPHIC VARIATION STUDY

			Av. Sp. Gr., g./cc.	
Area	Stand	Tree Numbers	Stands	Areas
A	1	T-79 to T-87-64	.433	.420
	2	T-89 to T-97-64	.417	
	3	T-98 to T-107-64	.400	
	4	T-108 to T-116-64	.424	
	5	T-118 to T-126-64	.427	
B	1	SP-2, SP-5, SP-6	.400	.392
	2	SP-3, SP-4, T-11 to T-13-62	.398	
	3	T-2 to T-10-62	.391	
	4	Clones 1, 2 & 7	.387	
	5	T-14 to T-22-62	.383	
C	1	T-7 to T-15-63	.382	.388
	2	T-16 to T-24-63	.391	
	3	T-25 to T-33-63	.375	
	4	Clones 12, 13 & 14	.393	
	5	Clones 20, 21 & 22	.402	
D	1	T-6 to T-14-64	.382	.374
	2	T-15 to T-23-64	.385	
	3	T-24 to T-32-64	.369	
	4	T-33 to T-35-64, T-50 & T-36 to T-40-64	.365	
	5	T-41 to T-49-64	.371	
E	1	T-34 to T-42-63	.376	.378
	2	T-43 to T-51-63	.369	
	3	T-51 to T-59-64	.387	
	4	T-60 to T-68-64	.379	
	5	T-69 to T-77-64	.380	

STUDIES OF VARIATION IN SPECIFIC GRAVITY

Specific gravity has been used as a criteria for parent tree selection for a number of years. Early comparisons indicated satisfactory correlations exist between specific gravity values obtained from breast high increment cores and whole tree specific gravity data. Data from disks taken in whole tree pulping studies at

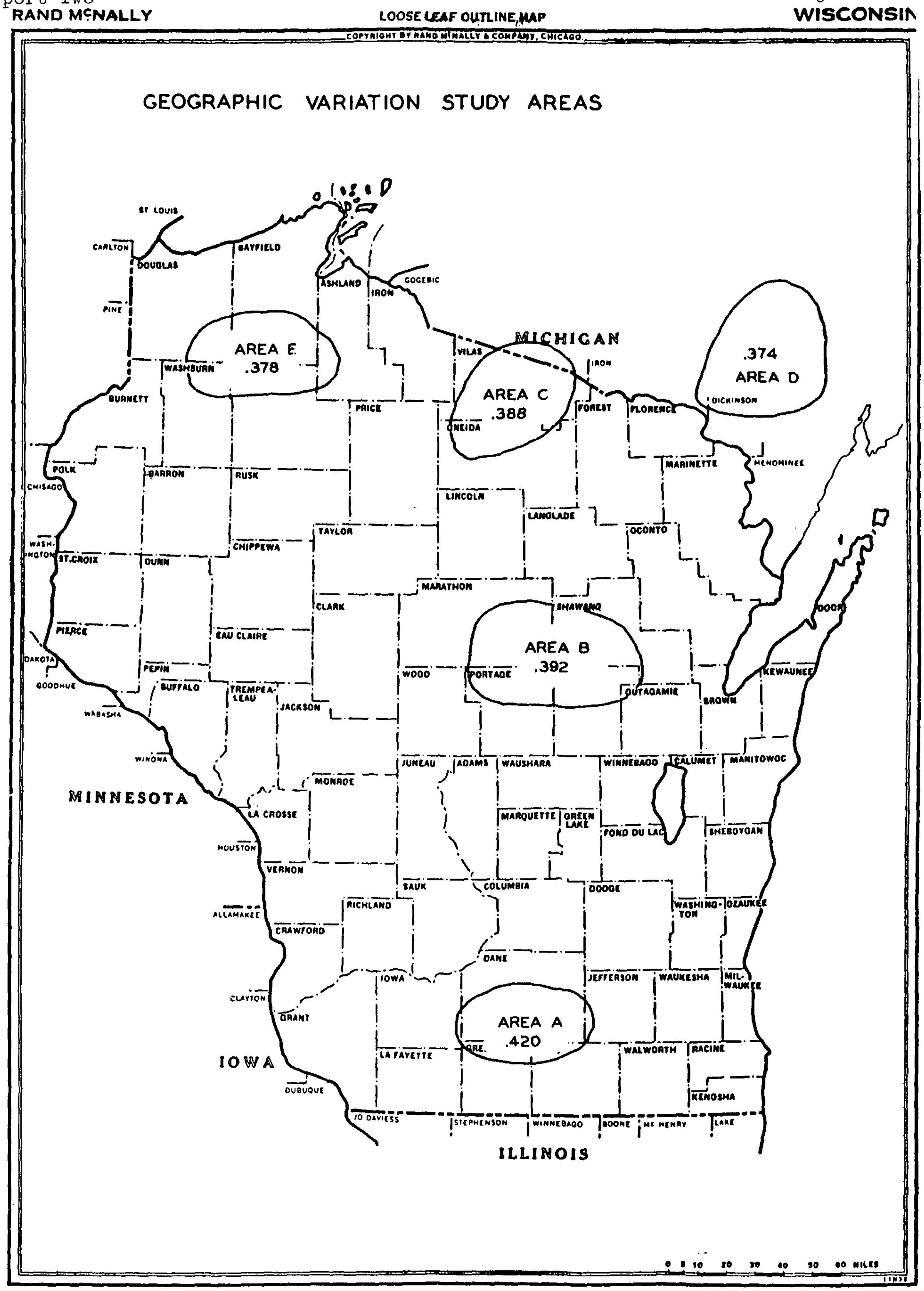

Figure 5. Illustrated Are the Specific Gravities of Study Areas Sampled in the Quaking Aspen Geographic Variation Study

varying heights along the stem demonstrated that specific gravity starts out relatively high at the two-foot level, gradually decreases until the 20-foot level, and then begins to increase again reaching a specific gravity approximately equal to the breast high specific gravity at 40 to 45 feet.

Specific gravity variation from the pith outward has been studied by a number of researchers including studies by Lenz (5) working with Italian hybrid poplars, Valentine (6) with *Populus tremuloides*, and Curro (7) with clones of *Populus* x *euramericana*. Lenz's work failed to turn up any consistent trends, while studies by Valentine and Curro demonstrated a trend of increasing specific gravity with increasing numbers of rings from the pith. Most species tend to level off in specific gravity between the twentieth and thirtieth annual rings. This same trend was assumed to exist for bigtooth and quaking aspen in the Lake States. Evaluation of the specific gravity of five-year-old aspen seedlings has raised some questions regarding the validity of such trends when considering the early growth rings of seedlings.

Examination of the specific gravity of a number of progeny groups which were a part of the natural variation studies described earlier, revealed five-year-old seedlings that had specific gravities equal to those of mature trees. This, of course, raises several questions including: (1) morphological reasons for high early specific gravity, (2) year-by-year trends in specific gravity of young seedlings, (3) relationship of year-by-year specific gravity trends for seedlings with year-by-year trends for root sprouts. To obtain answers to these questions, several small interrelated studies have been undertaken and will be completed over the next two-year period. The results of the first two such studies are described in the sections that follow.

Morphological Comparison of Seedling Specific Gravity Variation*

Disks from six five-year-old seedlings that varied in specific gravity were sectioned and slides prepared of representative cross sections of annual rings four and five. These slides were examined and descriptions made of the abnormalities encountered in an effort to determine the major reasons for the specific gravity variation observed. Table VII lists the trees studied, the specific gravity variation involved, and the apparent reasons for this variation.

The trees listed in Table VII are seedlings from Experimental Trial X located on the Ripco Experimental Farm near Eagle River, Wisconsin. Trial X is a replicated trial growing on a uniform sandy site and all seedlings except XT-Ta-14-58, A-3, were from the same replication (Block D). The seedlings of experimental cross XT-12-58 are diploid and were produced by crossing two selected diploid quaking aspen trees. Seedlings of experimental cross XT-Ta-14-58 are triploid and were produced by crossing a diploid (2n) female quaking aspen from Upper Michigan with a tetraploid (4n) male European aspen growing in Sweden. As is evident from the descriptions presented in the table of data, higher than average specific gravity** can result from several causes and extremely high or extremely low values very likely are the result of a combination of factors. Higher than average specific gravity, based on the observations described in the data table can result from: (1) presence of large numbers of gelatinous fibers associated with reaction wood, (Fig. 6), (2) small and/or few vessel elements per unit area (Fig. 7), (3) annual rings containing a large proportion of narrow, thick-walled tracheids (Fig. 7), and (4) a combination of the above factors (Fig. 6). Based on the observations de-

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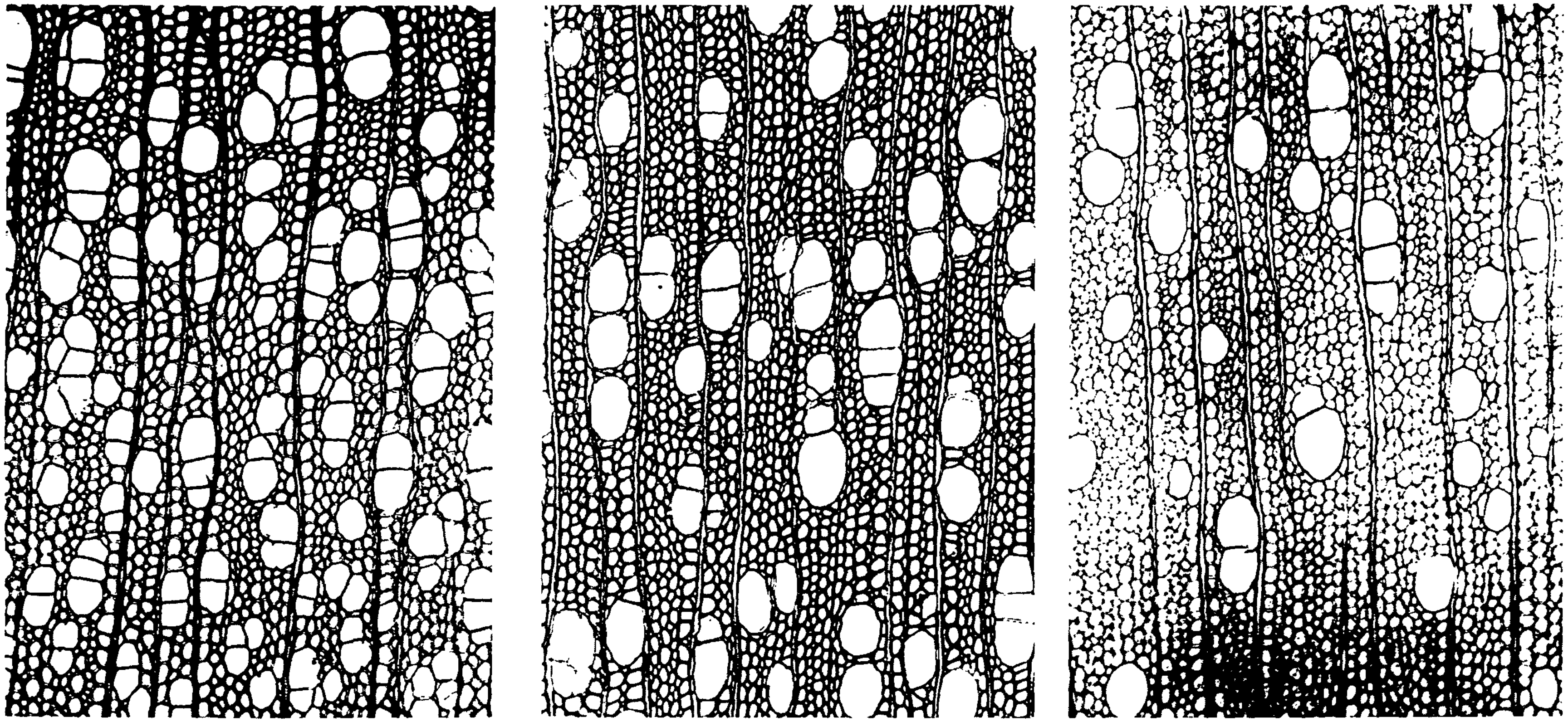
*Slides, observations, and photographs were made by John Hankey of the Fiber Microscopy Section.

**Average specific gravity for mature trees in northern Wisconsin is .38 to .39.

TABLE VII

SUMMARY OF OBSERVATIONS ON SPECIFIC GRAVITY VARIATION

Tree No.	Sp. Gr., g./cc.	Height, feet	Diameter, inches	Observations on Annual Rings 4 and 5
XT-12-58, D-1	.325	14.8	2.1	Ring 4 – Scattered groups of gelatinous fibers, vessels larger than average. Ring 5 – Scattered groups of gelatinous fibers, vessels numerous and much larger than average. Fiber cell wall thickness less than average.
XT-12-58, D-2	.442	14.5	1.0	Ring 4 – Scattered gelatinous fibers, diameter of springwood and summerwood fibers less than average and cell walls are thicker than normal. Vessel diameters also less than average. Ring 5 – Very few scattered gelatinous fibers, diameter of springwood fibers, summerwood fibers and vessels about average, cell walls thicker than average.
XT-Ta-14-58, A-3	.347	17.5	1.8	Rings 4 and 5 – Contain only a few scattered gelatinous fibers, number vessels per unit area and average diameter of vessels greater than other individuals examined from this cross.
XT-Ta-14-58, D-12	.375	28.0	3.2	Rings 4 and 5 – Contain very few scattered gelatinous fibers; fiber diameter, fiber cell wall thickness and vessel size and number appear normal.
XT-Ta-14-58, D-13	.420	22.0	2.7	Ring 4 – Numerous gelatinous fibers in the springwood and early summerwood areas. Ring has fewer than average vessels per unit area. Ring 5 – 80-90% of area of this ring made up of gelatinous fibers. Vessels per unit area are about average.
XT-Ta-14-58, D-5	.424	26.0	2.7	Ring 4 – Band of gelatinous fibers 90 cells wide in summerwood section of ring. Other cell dimensions normal. Ring 5 – With the exception of last formed summerwood fibers, gelatinous fibers abundant through the growth ring. Springwood growth almost 100% gelatinous fibers.



.347 .375 .420

Figure 6. Comparable Cross Sections of Three Triploid Aspen Hybrids Having Specific Gravities of .347, .375, and .420. Above Average Number Vessels Plus Above Average Width of Tracheids Resulted in Low Specific Gravity (.347). Relatively Few Vessels and Large Numbers of Gelatinous Fibers Resulted in Abnormally High Specific Gravity (.420)

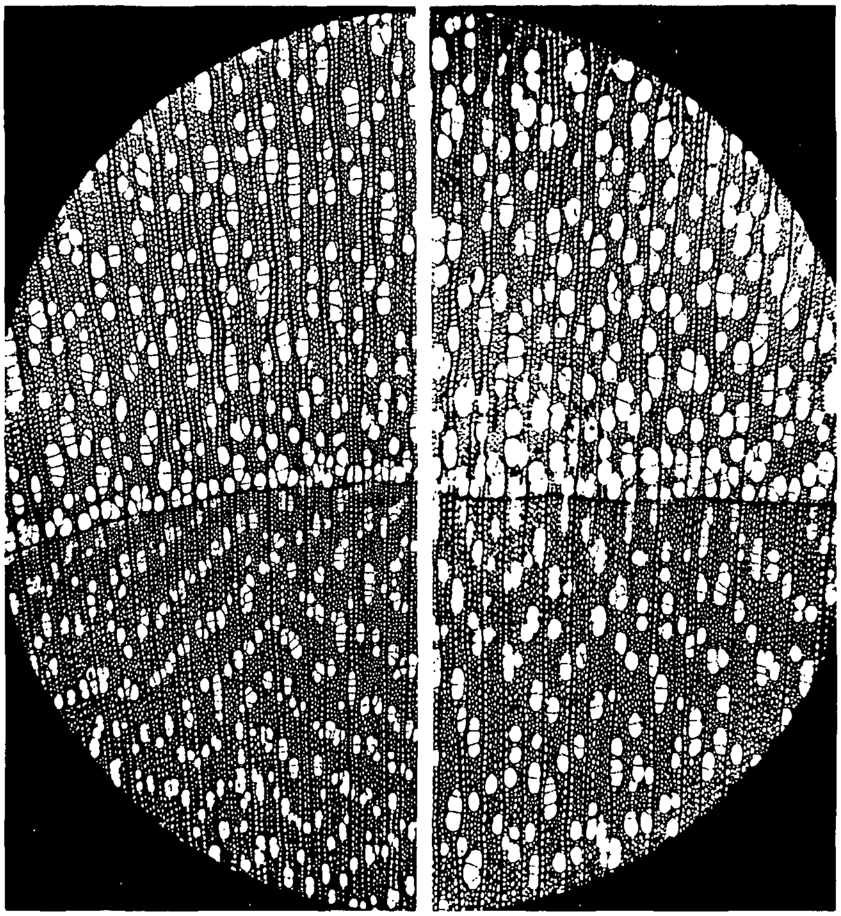


Figure 7. Comparable Cross Sections of Annual Rings 4 and 5 Illustrates Reason for Large Specific Gravity Differences. The Aspen on the Left (Specific Gravity .442) Has a Small Total Area Occupied by Vessels and Narrow Thick-Walled Tracheids. The Tree on the Right (Specific Gravity .325) Has a Large Area Occupied by Vessels and Many Wide Thin-Walled Tracheids

scribed in this study, it appears that when abnormal specific gravity values are obtained in the evaluation of parent trees and progeny, it would be appropriate to investigate further the causes for such variation. Sectioning and microscopic examination appears to be an appropriate technique for such work.

Specific Gravity-Age Trends in Young Aspen Seedlings

To investigate early changes in the specific gravity of aspen seedlings with increasing age, 20 five-year-old seedlings (10 trees from two progeny groups) were sampled. The two progeny groups, XT-7-58 and XT-12-58, were produced by controlled crosses between selected P. tremuloides parent trees and were part of Experimental Trial VII growing at the Institute's Greenville Farm. Trees involved were cut, disks obtained, and the disks sectioned on a ring by ring basis. The specific gravity information obtained was compared with specific gravity data from wedges containing all five annual rings. These data were also compared with ring width and diameter growth in an attempt to evaluate the influence of diameter growth on specific gravity. The specific gravity data presented is based on oven-dry weight divided by green volume.

Table XIV of the Appendix summarizes the data taken on each of the 20 trees involved in the study. Examination of these data demonstrates that specific gravity differences between annual rings are relatively small and the trend of specific gravity with age varies from tree to tree. In a number of the individuals investigated, the specific gravity of the first two annual rings was greater than that of ring number 5. This pattern was not consistent, however, and when the ring by ring specific gravity values for the twenty trees in the two progeny groups were averaged, there was essentially no difference in specific gravity with increasing number of rings from the pith. Figure 8 illustrates this point. Progeny from Experimental Cross XT-7-58 had an average specific gravity of .388 and exhibited a slight decreasing trend in specific gravity with age. Progeny from XT-12-58 had an average of .364 and had a slight trend of increasing specific gravity with age. In neither case were the trends statistically significant.

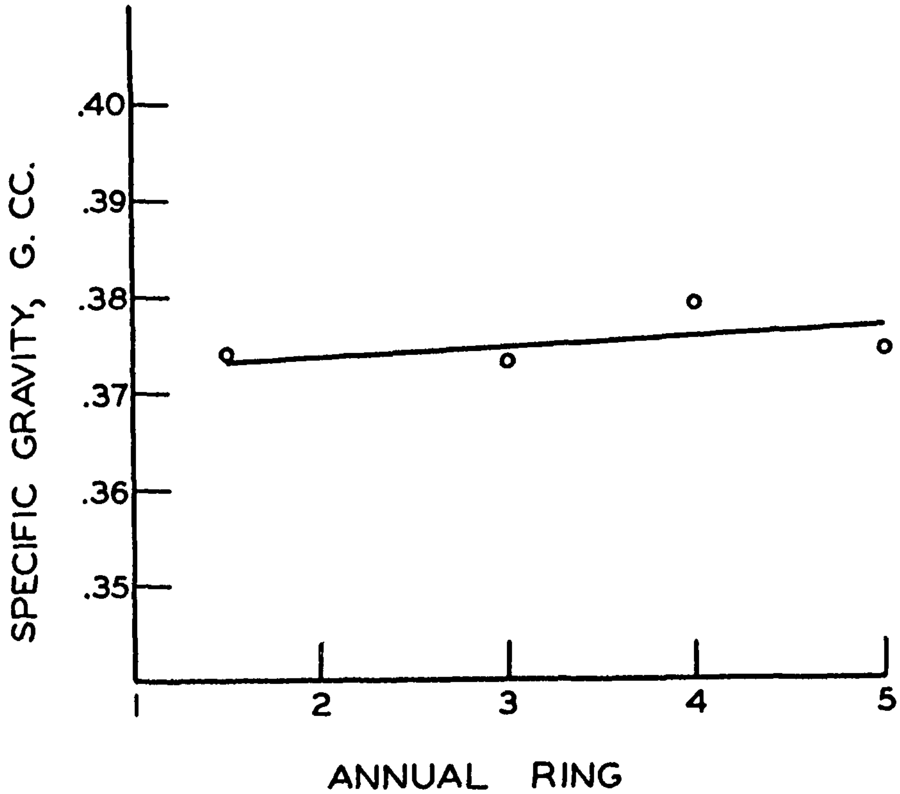


Figure 8. Specific Gravity Variation of Quaking Aspen for Rings One Through Five. Values Based Upon Measurements Taken on 20 5-Year-Old Seedlings

Evidence in the literature is conflicting regarding the relationship between diameter growth and specific gravity. Generally, however, it is believed that lower specific gravity is associated with rapid growth. This is particularly believed to be true if clonal material (genetically identical material) is grown at varying growth rates and comparable materials investigated.* To look into this relationship from the point of view of seedling progeny groups, the width of the fifth annual ring of each tree was compared with the specific gravity of the fifth annual ring. Also, the correlation between the radius of the wedge

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*It is hoped that this aspect of the specific gravity picture can be investigated when the new plant growth chamber is in operation.

sample which contained all five annual rings and the specific gravity of the wedge was examined. Table VIII summarizes the several correlations obtained.

TABLE VIII

CORRELATION COEFFICIENTS FOR SPECIFIC GRAVITY AND DIAMETER GROWTH DATA

Variables		r[a]
Specific gravity, wedge	Av. specific gravity, Rings 1 through 5	.95
	Specific gravity, Ring 5	.84
	Width Ring 5	.18
	Radius of wedge	.00
Av. specific gravity, Rings 1 through 5	Specific gravity, Ring 5	.77
	Width of Ring 5	.00
	Radius of wedge	-.17
Specific gravity, Ring 5	Width Ring 5	.38
	Radius of wedge	.27
Width of Ring 5	Radius of wedge	.73

[a] r values (correlation coefficients) are considered significant at the 5% level when they fall between .44 and .56 and significant at the 1% level for values greater than .56.

A good correlation was obtained when specific gravity values obtained from wedge samples were compared with the over-all average specific gravity of the five annual rings. The specific gravity of the fifth annual ring was well correlated with the wedge and average specific gravity data, indicating any one of the three types of samples would provide a satisfactory estimate of seedling specific gravity. No correlation was obtained between the width of Ring 5 and the specific gravity of Ring 5 or the radius of the wedge sample and the specific gravity of this same sample. Examination of several of the high specific gravity samples in this study suggests that reaction wood (gelatinous fibers) appears to be an important modifying factor influencing specific gravity — rate of growth relationships. Observations obtained so far in these investigations indicate that rapid growing individuals with high specific gravity do occur and it appears that the specific gravity of these individuals can be further modified by environmental manipulation.

INTRASPECIFIC AND INTERSPECIFIC CROSSING

The 1964 crossing program continued to strive toward the earlier discussed goals of producing individuals with satisfactory growth and above average wood quality for use on three types of soil-site situations. These goals include the production of quaking aspen crosses and triploid quaking aspen suitable for use on medium-textured hardwood sites; bigtooth aspen crosses and bigtooth aspen hybrids for use on dry sandy sites; and cottonwood selections and crosses for moist site conditions.

During 1964, 28 parent trees were employed in the crossing program and a total of 36 experimental crosses were attempted. Major emphasis was again placed on producing bigtooth aspen crosses and bigtooth aspen hybrids. The crossing of cottonwood was also emphasized with a total of 9 crosses being attempted. Lack of a simple, easily applied crossing technique for cottonwood continues to hamper the rapid expansion and large-scale production of seedlings for this phase of the program. Bigtooth aspen, quaking aspen, European white poplar, European gray poplar, European aspen, and eastern cottonwood were the species of Populus used as parent trees. Table IX summarizes the parent trees utilized in the crossing program and Tables X and XI provide additional information on crossing success, seedling size, and seedling production.

The crosses were conducted in the greenhouse in three groups or series and a large percentage of the seedlings were grown in outdoor seedbeds at the Institute's Greenville Nursery. The first series of crosses was made in early February and employed the quaking aspen parent trees. The second series involved the bigtooth aspen parent trees and was conducted in March. The cottonwood crosses, which made up the last phase of the program, were conducted in April.

TABLE IX

SUMMARY OF CROSSES AND LOCATION OF PARENT TREES

Cross No.[a]	Parents (female x male)		
XT-1-64	T-1-58 (Porcupine Mts., Mich.)	X	T-13-58 (Clintonville, Wis.)
XT-2-64	T-1-58 (Porcupine Mts., Mich.)	X	XT-22-56, No. 14 (Greenville, Wis.)
XT-3-64	XT-11-57, No. 4 (Greenville, Wis.)	X	XT-22-56, No. 14 (Greenville, Wis.)
XT-4-64	XT-22-56, No. 43 (Greenville, Wis.)	X	XT-32-56, No. 53 (Greenville, Wis.)
XT-5-64	T-1-58 (Porcupine Mts., Mich.)	X	T-6-61 (Fern, Wis.)
XT-Ta-6-64	T-1-58 (Porcupine Mts., Mich.)	X	Ta-10 (4n) (Ekebo, Sweden)
XG-7-64	G-12-60 (Black River Falls, Wis.)	X	G-2-58 (Porcupine Mts., Mich.)
XG-8-64	G-12-60 (Black River Falls, Wis.)	X	G-19-62 (Cornell, Wis.)
XG-9-64	G-12-60 (Black River Falls, Wis.)	X	G-8-63 (Hiles, Wis.)
XG-10-64	G-10-62 (Bonita, Wis.)	X	G-2-58 (Porcupine Mts., Mich.)
XG-11-64	G-10-62 (Bonita, Wis.)	X	G-19-62 (Cornell, Wis.)
XG-12-64	G-10-62 (Bonita, Wis.)	X	G-8-63 (Hiles, Wis.)
XG-13-64	G-9-63 (Bruce, Wis.)	X	G-2-58 (Porcupine Mts., Mich.)
XG-14-64	G-9-63 (Bruce, Wis.)	X	G-19-62 (Cornell, Wis.)
XG-15-64	G-9-63 (Bruce, Wis.)	X	G-8-63 (Hiles, Wis.)

Note: For footnote see end of table.

TABLE IX (Continued)

SUMMARY OF CROSSES AND LOCATION OF PARENT TREES

Cross No.[a]	Parents (female x male)		
XCa-G-16-64	Ca-2 (Czechoslovakia)	X	G-2-58 (Porcupine Mts., Mich.
XCa-G-17-64	Ca-2 (Czechoslovakia)	X	G-19-62 (Cornell, Wis.)
XCa-G-18-64	Ca-2 (Czechoslovakia)	X	G-8-63 (Hiles, Wis.)
XCa-G-19-64	Ca-2 (Czechoslovakia)	X	G-1-58 (Porcupine Mts., Mich.
XA-G-20-64	A-1-62 (Orfordville, Wis.)	X	G-2-58 (Porcupine Mts., Mich.
XA-G-21-64	A-1-62 (Orfordville, Wis.)	X	G-19-62 (Cornell, Wis.)
XA-G-22-64	A-1-62 (Orfordville, Wis.)	X	G-8-63 (Hiles, Wis.)
XG-A-23-64	G-10-62 (Bonita, Wis.)	X	A-1, No. 4 (Institute of Paper Chemistr
XD-24-64	D-2-63 (Sherwood, Wis.)	X	D-1-61 (Calumet County, Wis.)
XD-25-64	D-2-63 (Sherwood, Wis.)	X	D-1-63 (Waupaca, Wis.)
XD-26-64	D-2-63 (Sherwood, Wis.)	X	D-2-64 (Bruce, Wis.)
XD-27-64	D-1-64 (Bruce, Wis.)	X	D-1-61 (Calumet County, Wis.)
XD-28-64	D-1-64 (Bruce, Wis.)	X	D-1-63 (Waupaca, Wis.)
XD-29-64	D-1-64 (Bruce, Wis.)	X	D-2-64 (Bruce, Wis.)

Note: For footnote see end of table.

TABLE IX (Continued)

SUMMARY OF CROSSES AND LOCATION OF PARENT TREES

Cross No.[a]	Parents (female x male)		
XD-30-64	D-3-64 (Greenwood, Wis.)	X	D-1-61 (Calumet County, Wis.)
XD-31-64	D-3-64 (Greenwood, Wis.)	X	D-1-63 (Waupaca, Wis.)
XD-32-64	D-3-64 (Greenwood, Wis.)	X	D-2-64 (Bruce, Wis.)
XT-Ta-33-64	T-29-57 (3*n*) (Bruce Crossing, Mich.)	X	Ta-10 (4*n*) (Ekebo, Sweden)
XT-A-34-64	T-1-58 (Porcupine Mts., Mich.)	X	A-1, No. 4 (low irradiation) (Institute of Paper Chemistry)
XT-A-35-64	T-1-58 (Porcupine Mts., Mich.)	X	A-1, No. 4 (medium irradiation) (Institute of Paper Chemistry)
XT-A-36-64	T-1-58 (Porcupine Mts., Mich.)	X	A-1, No. 4 (high irradiation) (Institute of Paper Chemistry)
XD-0-37-64	D-4-64 (Appleton, Wis.)	X	Wind

[a]X = cross, A = *P. alba*, Ca = *P. canescens*, D = *P. deltoides*, G = *P. grandidentata*, T = *P. tremuloides*, Ta = *P. tremula*.

Additional details of these three series of crosses are presented in a discussion that follows.

QUAKING ASPEN CROSSES

Quaking aspen crosses received major emphasis in the early phases of the Institute's tree improvement work and a large number of crosses involving quaking aspen parent trees have been field planted. These experimental crosses are in the process of being evaluated and, as more and more information is accumulated, outstanding crosses will be repeated for wider planting and outstanding individuals within the crosses selected for vegetative propagation and for future crossing work. Pending evaluation of these earlier trials, emphasis on quaking aspen crossing has been reduced.

Five quaking aspen crosses (XT-1-64 through XT-5-64) were completed in 1964 and in addition quaking aspen parent trees were used in five interspecies crosses. These latter crosses were being made as part of the earlier described investigations being conducted on the ways of producing haploid (1n), triploid (3n), and tetraploid (4n) trees.

Of particular interest in this group of quaking aspen crosses are XT-2-64, XT-3-64, and XT-4-64. These crosses employed as parent trees selected progeny produced from earlier studies conducted at the Institute in 1956 and 1957. This marks the first chance to use selected individuals from some of the better early experimental crosses. The parent trees in this series handled well and seed and seedling production was satisfactory. Plans for the use of the trees produced involve testing on IPC Test Sites and in co-operator plantings.

BIGTOOTH ASPEN CROSSES

This rather general group of experimental crosses includes genetic combinations between selected bigtooth aspen parent trees and hybrids* produced by crossing bigtooth aspen with European gray poplar and European white poplar. Seventeen crosses were attempted in which bigtooth aspen were used as one or both parent trees. The principal objectives of this crossing work included the production of

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*The general term cross as used in a report refers to crosses within species and the term hybrid is used for crosses between different species.

TABLE X

SUMMARY OF 1964 CROSSES

Cross No.[a]	Type Cross[b]	No. of Catkins Pollinated	No. of Catkins Collected	Amt. Seed[c]	Seeds/Catkin[c]	Germ., %[c]
XT-1-64	C	105	103	36,630	341	96
XT-2-64	C	72	69	6,145	87	98
XT-3-64	C	7	7	750	105	98
XT-4-64	C	5	5	2,320	454	98
XT-5-64	C	127	115	14,630	127	100
XT-Ta-6-64	C-P	125	125	17,850	142	100
XG-7-64	DS	65	33	3,600	65	60
XG-8-64	DS	102	61	2,310	16	42
XG-9-64	DS	80	25	3,690	100	68
XG-10-64	DS	48	46	11,820	243	94
XG-11-64	DS	45	41	24,730	512	85
XG-12-64	DS	45	29	16,130	472	85
XG-13-64	DS	52	36	4,660	56	44
XG-14-64	DS	57	51	12,870	176	70
XG-15-64	DS	46	41	10,020	210	86
XCa-G-16-64	DS	57	53	11,790	209	94
XCa-G-17-64	DS	54	52	5,280	96	95
XCa-G-18-64	DS	50	48	10,630	210	95
XCa-G-19-64	DS	48	48	8,760	162	89
XA-G-20-64	DS	55	16	2,930	46	25
XA-G-21-64	DS	40	8	1,850	6	3
XA-G-22-64	DS	45	3	1,440	14	3
XG-A-23-64	DS	60	55	10,278	104	56
XD-24-64	B	30	18	4,806	74	28
XD-25-64	B	10	1	258	232	90
XD-26-64	B	9	0	—	—	—
XD-27-64	B	10	0	—	—	—
XD-28-64	B	11	1	13	10	77
XD-29-64	B	10	0	—	—	—
XD-30-64	B	9	3	460	80	52
XD-31-64	B	9	3	452	20	14
XD-32-64	B	9	2	168	32	40
XT-Ta-33-64	P	25	24	902	4	13
XT-A-34-64	H	3	3	803	91	34
XT-A-35-64	H	3	3	827	99	36
XT-A-36-64	H	4	4	806	91	34

[a]X = cross, A = P. alba, Ca = P. canescens, D = P. deltoides, G = P. grandidentata, T = P. tremuloides, Ta = P. tremula. [b]C = Seed for semicommercial production, DS = dry site cross, B = crosses in black poplar group, P = polyploid crosses, H = haploid crosses. [c]Amount of seed, no. viable seeds/catkin collected and germination % based upon 40 and 50-mesh seed for all crosses except XT-1, 2, 4, 5-64 and XT-Ta-6-64, which were based upon 40-mesh seed only.

TABLE XI

SUMMARY OF 1964 SEEDLING PRODUCTION

Cross No.[a]	Total No. Seeds Planted	Total No. Seedlings Produced	No. Plantable Seedlings[b] Misc. Beds	Repl. Beds	Av. Height[c] All Seedlings	Plantable Seedlings
XT-1-64	800	280	238	–	–	–
XT-2-64	1200	825	218	500	1.8	1.9
XT-3-64	750	368	–	345	1.8	1.8
XT-4-64	1200	526	–	500	1.6	1.7
XT-5-64	2700	1005	219	425	1.8	1.9
XT-Ta-6-64	10800	4830	2971	415	1.6	1.7
XG-7-64	3600	420	106	220	1.4	1.6
XG-8-64	2310	290	–	215	1.3	1.6
XG-9-64	3690	470	128	215	1.4	1.6
XG-10-64	3660	1050	248	195	1.6	1.8
XG-11-64	5200	1081	564	345	1.8	2.0
XG-12-64	5100	1025	407	325	1.6	1.8
XG-13-64	4660	565	102	250	1.4	1.6
XG-14-64	5565	965	297	415	1.8	2.0
XG-15-64	3598	646	115	350	1.7	1.8
XCa-G-16-64	3200	2040	1157	610	2.2	2.4
XCa-17-64	4000	1315	537	545	2.0	2.1
XCa-G-18-64	5600	1755	1182	348	2.0	2.2
XCa-G-19-64	5600	1415	851	360	2.3	2.4
XA-G-20-64	2930	130	–	120	2.0	2.2
XA-G-21-64	1850	56	–	50	1.9	2.0
XA-G-22-64	1440	42	–	35	1.6	1.8
XG-A-23-64	10278	642	325	245	2.4	2.4
XD-24-64	4806	690	–	680	2.4	2.4
XD-25-64	258	115	–	110	2.2	2.2
XD-30-64	460	120	–	120	3.0	3.0
XD-31-64	452	31	–	29	2.3	2.4
XD-32-64	168	34	–	34	3.2	3.2
XT-Ta-33-64	902	119				
XT-A-34-64	803	15	(Only abnormal seedlings saved)			
XT-A-35-64	827	24	(Only abnormal seedlings saved)			
XT-A-36-64	806	46	(Only abnormal seedlings saved)			
XD-O-37-64						

[a]X = cross, A = P. alba, Ca = P. canescens, D = P. deltoides, G = P. grandidentata, T = P. tremuloides, Ta = P. tremula.
[b]Number of plantable seedlings, 1.0 ft. in height and of satisfactory caliper.
[c]Average heights based upon seedlings in replicated seedbeds; when replicated beds were not available, miscellaneous seedbeds were measured.

trees for "dry site" test plantings and the evaluation of the combining ability and over-all usefulness of the parent trees involved. Past experience with bigtooth aspen crosses has been characterized by low seed production and low seed germination. Seed production and germination in the 1964 bigtooth aspen crosses were well above average. The major exceptions to this statement were those crosses involving A-1-62 as a parent. A-1-62 is a bisexual tree and is also thought to be a natural hybrid. It is entirely possible that these factors may have influenced the crossing behavior of this tree.

A series of modified diallel crosses were used to evaluate the combining ability and over-all usefulness of five female and three male trees. Flowering behavior, seed and seedling production, and first-year seedling growth were used as criteria for evaluating the above parent trees. Table XII illustrates the results obtained when the parent trees were compared. Trees G-10-62 and Ca-2 were found to be the best two female trees evaluated. Male trees G-2-58 and G-8-63 behaved in a satisfactory manner and when crossed with the best two females, had good seedling production and produced progeny with satisfactory first-year growth. The performance of G-10-60 is of interest because this tree was evaluated in 1962 with a different group of male trees and ranked high in this earlier evaluation. Field planting of large numbers of the best progeny from this group of crosses is planned.

COTTONWOOD CROSSES

Slow development of the female flowers both prior to pollination and after pollination has made it difficult to bring the developing catkins through to maturity. Previous trials demonstrated that by grafting a female cottonwood scion, having a single flower bud, on to a one-year-old understock, the flower bud would open while the union between the scion and understock was taking place. By pollinating the receptive catkin and taking proper care of the flowering graft, approximately 30% of the developing catkins could be carried through to maturity.

TABLE XII

SUMMARY OF SEED AND SEEDLING PRODUCTION AND SEEDLING GROWTH
MODIFIED DIALLEL CROSSING SERIES

Female Parent Trees	Male Parent Trees		
	G-2-58	G-19-62	G-8-63
G-12-60	XG-7-64	XG-8-64	XG-9-64
a	33	10	31
b	5.0	2.1	4.3
c	1.4	1.3	1.4
G-10-62	XG-10-64	XG-11-64	XG-12-64
a	234	465	305
b	30	96	51
c	1.6	1.8	1.6
G-9-63	XG-13-64	XG-14-64	XG-15-64
a	39	157	188
b	6.8	29	28
c	1.4	1.8	1.7
Ca-2	XCa-G-16-64	XCa-G-17-64	XCa-G-18-64
a	194	92	202
b	114	26	58
c	2.2	2.0	2.0
A-1-62	XA-G-20-64	XA-G-21-64	XA-G-22-64
a	13	1.1	1.0
b	2.2	1.1	0.78
c	2.0	1.9	1.6

[a]Number of viable seeds produced per catkin pollinated.
[b]Number of plantable seedlings (1.0 feet plus) produced per catkin pollinated.
[c]Average height of all seedlings in seedbeds.

Using the technique described above, a modified diallel crossing series, similar to that described for bigtooth aspen, was established to evaluate the combining ability, seedling production, and seedling growth of three male and three female parent trees. The use of such a grafting procedure complicates the interpretation of results because late failures of graft unions would reduce seed production and this would have nothing to do with the combining ability of the two parent trees being evaluated. Usually, however, most grafts fail prior to pollination and only the occasional late failures influence the results obtained.

Table XIII summarizes the results of this series of crosses and Fig. 9 illustrates one-year-old cottonwood seedlings growing in seedbeds at the Greenville Nursery. Seed and seedling production was not high for any of the crosses. D-1-61 turned out to be the male with the best combining ability and D-3-64 was the best female tree. D-2-64, a male selection of outstanding size growing near Bruce, Wisconsin, and D-1-64, a female from the same location, were the trees with the poorest combining ability. The extreme northern location of these trees may be the cause for the poor flower bud development that was noted.

Plans for handling the cottonwood seedlings include the selection and propagation of the outstanding one or two per cent of the individuals produced in each cross, and the field testing in replicated trials of the best remaining forty to fifty per cent. Additional cottonwood crosses and tests are planned for the coming two or three years.

TABLE XIII

SUMMARY OF SEED AND SEEDLING PRODUCTION AND SEEDLING GROWTH
MODIFIED DIALLEL CROSSING SERIES

Female Parent Trees	Male Parent Trees		
	D-1-61	D-1-63	D-2-64
D-2-63	XD-24-64	XD-25-64	XD-26-64
a	44	24	0
b	23	11	0
c	2.4	2.2	–
D-1-64	XD-27-64	XD-28-64	XD-29-64
a	0	1.0	0
b	0	0	0
c	–	–	–
D-3-64	XD-30-64	XD-31-64	XD-32-64
a	26	6.6	7.2
b	13	3.2	3.6
c	3.0	2.3	3.2

[a] Number of viable seeds produced per catkin pollinated.
[b] Number of plantable seedlings (1.0 feet plus) produced per catkin pollinated.
[c] Average height of all seedlings in seedbeds.

Figure 9. One-Year-Old Cottonwood Seedlings Produced From Controlled Crosses Made in 1964

PLANS FOR 1965

During 1965 the emphasis of Project 2412 work will continue to be directed toward four main areas of investigation. These areas of investigation will include: (1) selection and hybridization, (2) production of artificial polyploids, (3) studies of natural variation with special emphasis on "wood quality," and (4) biochemical characterization of aspen clones and aspen hybrids. The only change in our over-all plans is the extensive use of the controlled environment "growth chamber" recently completed. The studies to be initiated in this new facility will fall into all four main areas described above and will be used to supplement field and greenhouse investigations.

Selection and hybridization studies will continue to emphasize the production of trees suitable for use in so-called "dry site" plantings. A considerable amount of effort will also be directed toward the production of cottonwood crosses suitable for use on "wet sites" in central and north central Wisconsin. Growth chamber runs are planned as a method of improving seed production of cottonwood crosses. Preliminary growth chamber studies are planned with the objective of determining the feasibility of using sand culture techniques to evaluate the nutrient requirements of aspen hybrids.

Investigations on methods of producing polyploids will be expanded to include studies on methods of producing polyploid bigtooth aspen and cottonwood. Use of the technique of treating "newly formed embryos" with colchicine will be the principal approach employed. Considerable emphasis will be placed on improving cytological techniques in order to obtain accurate chromosome numbers on tetraploid prospects produced by earlier studies.

Two investigations presently under way in the area of natural variation include: (1) the heritability of wood and growth characteristics of quaking aspen, and (2) the quaking aspen geographic variation study. The field aspects of this latter study have been completed and the laboratory phases of the work are well under way. Work on these studies is to be continued and will provide information on natural variation and heritability of growth and "wood quality" characteristics.

Investigations in the area of biochemical characterization of aspen clones and aspen hybrids will be handled in a separate report and the plans for this phase of the project work will be discussed in detail in this report.

PUBLICATIONS

PUBLICATIONS RELATING TO PROJECT 2412 AND ALLIED PROJECTS SINCE MAY, 1964

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8. Gardner, H. S., and Einspahr, D. W. Reproducibility of micropulping wood samples. Tappi 47:432-4(July, 1964).

FUTURE PUBLICATIONS

1. Benson, M. K., Einspahr, D. W., and Schwalbach, D. E. Rooting of quaking aspen root sprouts. To be submitted to Tree Planters' Notes.

2. Benson, M. K., and Einspahr, D. W. Growth comparisons of naturally occurring and artificially produced triploid aspen with diploid aspen. To be submitted to Journal of Forestry.

3. Einspahr, D. W., and Benson, M. K. Comparison of wood, fiber and pulp properties of naturally occurring and artificially produced triploid aspen with diploid aspen. To be submitted to Tappi.

4. Einspahr, D. W., and Winton, L. W. Colchicine treatment of newly-formed embryos of quaking aspen. To be submitted to Forest Science.

5. Einspahr, D. W., Benson, M. K., and Peckham, J. R. Geographic variation in growth and wood properties of quaking aspen. To be submitted to Journal of Forestry or Forest Science.

6. Mathes, M. C., and Einspahr, D. W. Comparison of tree growth and callus production in aspen. Submitted to Forest Science.

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TABLE XIV

SUMMARY OF ANNUAL RING SPECIFIC GRAVITY MEASUREMENTS

Tree No.	Annual Ring Sampled[a]	Sp. Gr., g./cc.	Av. Sp. Gr., g./cc.	Ring Width or Wedge Radius, mm.
XT-7-58	1 & 2	.393		–
No. 6	3	.390	.388	–
	4	.378		–
	5	.389		5.5
	Wedge (1-5)		.384	20.0
No. 10	1 & 2	.380	.390	–
	3	.386		–
	4	.396		–
	5	.396		5.0
	Wedge (1-5)		.404	16.8
No. 15	1 & 2	.367	.368	–
	3	.362		–
	4	.362		–
	5	.380		4.0
	Wedge (1-5)		.372	18.0
No. 17	1 & 2	.403	.390	–
	3	.392		–
	4	.389		–
	5	.376		3.2
	Wedge (1-5)		.381	13.0
No. 26	1 & 2	.372	.373	–
	3	.372		–
	4	.366		–
	5	.382		4.5
	Wedge (1-5)		.375	21.0
No. 28	1 & 2	.442	.398	–
	3	.393		–
	4	.380		–
	5	.378		4.0
	Wedge (1-5)		.392	14.0
No. 32	1 & 2	.379	.374	–
	3	.360		–
	4	.378		–
	5	.382		3.2
	Wedge (1-5)		.374	16.2

Note: See end of table for footnote.

TABLE XIV (Continued)

SUMMARY OF ANNUAL RING SPECIFIC GRAVITY MEASUREMENTS

Tree No.	Annual Ring Sampled[a]	Sp. Gr., g./cc.	Av. Sp. Gr., g./cc.	Ring Width or Wedge Radius, mm.
XT-7-58 No. 37	1 & 2	.389	.382	–
	3	.378		–
	4	.384		–
	5	.380		3.2
	Wedge (1-5)		.390	13.0
No. 41	1 & 2	.418	.416	–
	3	.419		–
	4	.428		–
	5	.400		4.0
	Wedge (1-5)		.412	14.5
No. 54	1 & 2	.381	.388	–
	3	.370		–
	4	.374		–
	5	.428		9.8
	Wedge (1-5)		.400	25.5
XT-12-58 No. 4	1 & 2	.346	.352	–
	3	.338		–
	4	.372		–
	5	.355		4.5
	Wedge (1-5)		.353	18.0
No. 8	1 & 2	.336	.342	–
	3	.329		–
	4	.354		–
	5	.352		5.5
	Wedge (1-5)		.350	23.0
No. 17	1 & 2	.329	.364	–
	3	.362		–
	4	.401		–
	5	.362		4.0
	Wedge (1-5)		.359	21.5
No. 26	1 & 2	.354	.344	–
	3	.362		–
	4	.350		–
	5	.310		5.0
	Wedge (1-5)		.346	15.0

Note: See end of table for footnote.

TABLE XIV (Continued)

SUMMARY OF ANNUAL RING SPECIFIC GRAVITY MEASUREMENTS

Tree No.	Annual Ring Sampled[a]	Sp. Gr., g./cc.	Av. Sp. Gr., g./cc.	Ring Width or Wedge Radius, mm.
XT-12-58	1 & 2	.358	.352	–
No. 28	3	.352		–
	4	.348		–
	5	.350		3.5
	Wedge (1-5)		.352	14.5
No. 30	1 & 2	.356	.360	–
	3	.338		–
	4	.386		–
	5	.360		3.5
	Wedge (1-5)		.366	11.0
No. 35	1 & 2	.374	.372	–
	3	.380		–
	4	.366		–
	5	.368		4.5
	Wedge (1-5)		.373	16.5
No. 37	1 & 2	.382	.392	–
	3	.413		–
	4	.396		–
	5	.375		4.0
	Wedge (1-5)		.389	17.0
No. 41	1 & 2	.382	.388	–
	3	.386		–
	4	.391		–
	5	.392		3.5
	Wedge (1-5)		.382	14.5
No. 48	1 & 2	.352	.372	–
	3	.376		–
	4	.380		–
	5	.380		4.5
	Wedge (1-5)		.376	20.0

[a]Rings 1 and 2 were combined because of size and difficulty of separation. Wedge-shaped samples contained Rings 1 through 5 and the values presented are the average of two determinations.

THE INSTITUTE OF PAPER CHEMISTRY

Appleton, Wisconsin

A STUDY OF THE GENETIC IMPROVEMENT OF QUAKING AND BIGTOOTH ASPEN BY SELECTION, HYBRIDIZATION, AND THE EXPLOITATION OF POLYPLOIDY

Project 2412

Report Two

A Progress Report

to

LOUIS W. AND MAUD HILL FAMILY FOUNDATION

May 20, 1965